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THE AUSTRALIAN FRUIT FLY PARASITOID *DIACHASMIMORPHA KRAUSSII* (FULLAWAY): MATING BEHAVIOR, MODES OF SEXUAL COMMUNICATION AND CROSSING TESTS WITH *D. LONGICAUDATA* (ASHMEAD) (HYMENOPTERA: BRACONIDAE: OPIINAE)

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Abstract.—We describe the mating behavior of *Diachasmimorpha kraussii* for the first time, and confirm with cross-mating tests the separate species status of *D. kraussii* and *D. longicaudata.* Flight cage experiments suggest that mating takes place on foliage and that a distance attractant pheromone is secreted by the females, and perhaps also by the males. The most obvious aspect of the sexual interaction between males and females is the wing vibration performed by males in the nearby presence (about 1 cm) of a conspecific virgin female. Wing vibration produces an acoustic signal critical to mating success, for wingless males could seldom mate. Experimental manipulations demonstrate that males vibrate their wings in response to a chemical associated with the female, but not present in males. The chemical appears to be associated with the cuticle, as it is present (as demonstrated by male behavior) in recently-killed females, and it can be stripped from these females with acetone. The interaction proceeds only if the female is receptive (starting 6–48 h after emergence) and when she adopts a particular stance. Receptive females stand still, fold both pairs of wings over the abdomen, hold their antennae back together over their wings and allow males to mount. Males continue tapping their antennae on the females' thoraces while intromission takes place. The mating sequence of *D. longicaudata* is generally similar to that of *D. kraussii*, but individuals of the two species did not mate in small cages, which confirms their species status. In crossing tests all males vibrated their wings, indicating that the female's cuticular chemicals are similar across species. No females in mixed pairs assumed the receptive stance, suggesting the acoustic signals differ across species.

Key Words.—Diachasmimorpha kraussii, Diachasmimorpha longicaudata, parasitoid, Braconidae, Tephritidae, acoustic signal, wing vibration, monandry, pheromone.

Understanding mating behaviour is central to accurate interpretation of the species limits of sexual organisms. This is particularly true when cryptic (sibling) species compelexes are suspected (Fernando & Walter 1997). The sexual communication mechanism, or Specific-Mate Recognition System (SMRS), comprises several steps, each of which serves a function subservient to the ultimate function of achieving fertilization (Paterson 1985). Although particular aspects of the SMRS of many insect species are well known, in only very few species have attempts been made to identify each step in the sequence (see Matthews 1975, Field & Keller 1993, Abeeluck & Walter 1997). An understanding of all steps is critical to assessment of species limits and the species status of different populations (Fernando & Walter 1997). Here we describe research on the parasitic wasp *Diachasmimorpha kraussii* (Fullaway) that allows us to develop a diagrammatic model of the communication modes associated with each step in the entire mating sequence of this species.

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Wasps in the genus *Diachasmimorpha* parasitize tephritid fruit flies. Several of the species resemble one another so closely that the morphological features used to distinguish them tend to grade into one another. For example, the Australian species *D. kraussii* resembles *D. longicaudata* (Ashmead), an Asian species, and is distinguished only by the combination of pale coloration and an unsculptured second abdominal tergite (Wharton & Gilstrap 1983). Such characters are often subtle in that they may be open to subjective interpretation, especially when the named species have allopatric distributions. In such cases, behavioral confirmation of species limits helps to provide confidence in the designated morphological features actually being diagnostic.

Understanding the mating behavior of opiine parasitoids may also yield practical benefits because of their value to biological control. Several species of opiines were transported to Hawaii for rearing and release against *Bactrocera dorsalis* (Hendel) and *Ceratitis capitata* Wiedemann, between 1947 and 1953, but not all could be successfully reared (Clausen et al. 1965). A problem with some of the species was the low incidence of successful mating, so a preponderance of male offspring was produced prior to those cultures dying out. Understanding the requirements for mating of these species is therefore important for successful mass rearing (Purcell 1998). Although *D. kraussii* was "eventually propagated" on *C. capitata* and released prior to 1953, it did not establish (Clausen et al. 1965). Whether there were problems in getting wasps of this species to mate was not, however, mentioned.

To date, nothing has been published on the mating behavior of *D. kraussii*. Our aim in investigating the SMRS of *D. kraussii* is to provide a first model of the complete mating sequence of an opiine parasitoid. We thus provide a basis for comparison of mating behavior across host associated populations and across allopatric populations of *Diachasmimorpha*. We also use the information obtained to investigate intersexual interactions between *D. kraussii* and *D. longicaudata* individuals.

Materials and Methods

The *D. kraussii* colony was established with about 35 pairs reared from *B. tryoni* (Froggatt) puparia derived from Brazilian cherries (*Eugenia uniflora* L.) collected in St Lucia, Brisbane, in November 1990. The identification of the wasps was confirmed by R. A. Wharton and specimens have been deposited in the collections of Texas A&M University, College Station and The University of Queensland. *Diachasmimorpha longicaudata* was obtained from the culture held at the Tropical Fruit and Vegetable Research Laboratory of the United States Department of Agriculture, Honolulu, Hawaii. Both parasitoids were reared on *B. tryoni* and the maintenance of host and parasitoid colonies is described elsewhere (Rungrojwanich & Walter 1999).

Unless otherwise stated, the males and females used in experiments were one and three day old virgins, respectively, and observations were made in a "mating unit" made up of two glass tubes (2.5 cm diam. × 4.5 cm), each with one end covered with fine muslin and the other end left open. Only one pair/mating unit was observed at a time, for no more than 10 min.

Description and Duration of Mating Behavior.—Observations were conducted to establish which sex displays observable signalling behaviors, the nature of

those behaviors and the duration of signalling and copulation. Before the wasps were brought together, each insect was allowed to settle for ten min in its own tube. The open ends of the tubes were then brought together to allow the male and female to approach one another. Time spent on wing vibration by males and in copulation were recorded (in seconds) with a stop-watch (n = 20 pairs). Observations were conducted at 25 ± 1°C and 60 ± 5% R.H.

Mate Location: Flight Cage Observations.—The site where mating partners usually meet in nature was assessed indirectly. Nine flowering and/or fruiting guava trees (2 m tall, each in a 30 cm diameter pot, all with young fruits and some with honeydew-secreting scale insects) were placed 45 cm apart in a 180 × 180 × 200 cm fly-screen cage in a glasshouse. Conditions varied from 22° C to 29° C and 60% to 96% R.H., typical of summer weather conditions in Brisbane. All observations were conducted between 09:00 h and 17:30 h.

In the first set of observations, six *D. kraussii* females were released into the flight cage and their behavior was observed and recorded for 15 min before a single male was introduced. The time taken before a mating pair came together was measured and all behaviors and interactions were recorded. Once mating had taken place, the mating pair was removed and a new female released to maintain numbers. Another male was released 15 min later. Nineteen females and 14 males were ultimately tested.

In a second set of identical observations six virgin males were released first, followed by a single female. Similar observations to those described above were made and the wasps were treated in the same way. Totals of 25 males and 20 females were observed.

Stimulus for Male Wing Vibration.—A series of experiments was conducted with dead females (at 25 ± 1° C and 50 ± 2% R.H.) to determine (i) whether wing vibration by males is stimulated by chemicals associated with the female, (ii) if stimulatory chemicals are cuticular or are under active control from within the insect and (iii) whether visual cues are involved. Unless otherwise stated, a new set of one day old males was used in each test. Each replicate was observed for no longer than 10 min. The occurrence of male wing vibration and copulation attempts were noted and the duration of intromission was recorded.

Initially, a set of controls was run to determine whether the mating units and acetone (used later as a solvent: see below) would, in themselves, have any effect on the behavior of *D. kraussii* males. Nine males were placed in clean mating units (one/unit) for 10 min of observation, then each one was placed for 10 min in a mating unit to which had been added 0.5 ml acetone that had been allowed to evaporate. Males were also tested for their responses to other males.

The distance between the wasps of each living pair (n = 22) was measured when the male started vibrating his wings (see below) in response to the female's presence. Males were similarly assessed against virgin females that had recently been killed by freezing (−10° C for 15 min). These same dead females were then soaked in 15 ml of acetone for 15 min and specimens were air dried for 1 h before again being exposed to males.

To test whether males would recognize females by their visual appearance, the ovipositors of females were removed before exposure to males (as ovipositor protrusion is the only general observable way in which females differ from conspecific males). The females with ovipositors removed were soaked in acetone

after the experiment and air dried for another exposure to males. Females recently killed by freezing were cut into two parts (head + thorax and abdomen) to investigate whether the factor that influences the behavior of conspecific males is specific to body part.

To investigate whether an internally-derived chemical (e.g., from a pheromone gland reservoir) influences male behavior, dead females were crushed on the side of mating units (two/unit), with a glass rod. The carcasses were then removed and a male was placed in each mating unit.

The duration for which dead females would remain attractive to conspecific males was investigated by exposing the same set of dead females (n = 10) to a new set of males daily, until no male responded to them.

Role of Male Wing Vibration.—The functional significance of male wing vibration was assessed by exposure of females to wingless males (at 27° C and 65 ± 2% R.H.). Males (n = 16) were immobilized at −10° C for five min before each wing was cut off, just above the base. To establish whether the cold treatment alone would affect the behavior of males negatively, a set of controls was run first. Ten males were cold immobilized as above, but their wings were not cut off before exposure to females.

Female Premating Period and Polyandry.—The age of females (all virgins) used to measure the premating period varied from six h after emergence to 25 days old, whereas all males were one day old. Individuals in each pair (n = 208 pairs altogether) were tested only once even if they did not mate on first exposure.

To establish whether *D. kraussii* females would mate more than once, they (n = 17) were each exposed to a different conspecific male. When mated, each female was transferred to a 10 × 10 × 15 cm perspex cage. Honey solution was provided as food. An "oviposition unit" (Rungrojwanich & Walter 1999) containing about 100 *B. tryoni* larvae was provided daily. Each of these previously-mated females was later exposed to another one day old conspecific male at seven, 15 and 20 days after the first mating. Because of the early death of some females, only six and three were alive on days 15 and 20, respectively.

Is Mating Strictly Diurnal?—To assess whether mating by *D. kraussii* is confined to daylight, the mating success of laboratory-reared wasps (n = 14) was observed at night under field conditions (Sir John Chandler Park, Indooroopilly, Brisbane, 21:00 h, 3 Feb 1993). Light intensity was measured with a system exposure meter (LUNASIX 3). During the experiment it was equal to 0.35 lux or 0.032 fc, and ambient conditions were 25.5° C and 77% R.H. Males in pairs that did not mate were separated from the females for immediate transfer to an illuminated laboratory for re-testing with each other.

Cross-mating Experiment.—The sexual interactions between *D. kraussii* and *D. longicaudata* individuals were tested in mating units. The number of mixed pairs that mated successfully (out of 20 pairs in each reciprocal cross) was recorded, as was the level of interaction between the sexes. A set of control crosses (n = 20 pairs of each species) was also observed. Each pair was placed together in a mating unit for a maximum of 10 min, or until mating was completed. *Diachasmimorpha kraussii* males and females used in the experiments were one and three days old, respectively, whereas both sexes of *D. longicaudata* were three days old. Each wasp was virgin and used only once, and experiments were conducted at 25 ± 1° C and 60 ± 5% R.H.

Results

Description and Duration of Mating Behavior.—All *D. kraussii* males (n = 16) showed a distinct behavioral sequence in the nearby presence (about 1 cm) of a conspecific virgin female. Each male made a protracted series of wing vibrations, which was continued after he mounted a receptive female. Males also tapped their antennae on the female's thorax during intromission and insemination. A few males (12.5%, n = 16), stopped wing vibration and antennal tapping before intromission was completed.

Receptive *D. kraussii* females stood still while the male vibrated his wings. Simultaneously, the females folded both pairs of wings over their abdomens and held their antennae back together over the wings (100%, n = 16). Other observations (see below) showed that if a female was not ready to mate, she continued to walk around and sometimes vibrated her wings. Her antennae were kept apart and pointed forward. Intromission was never successful when a male tried to copulate with a female that had not assumed the appropriate posture.

The mean (± SE) time spent in copula was 23.7 (± 3.19) sec (n = 20), and in precopulatory courtship it was much less, at 8.8 (± 1.29) sec (n = 20).

Mate Location: Flight Cage Observations.—When virgin females were released into the cage before males, they flew directly to the plants and each landed on the upper surface of a leaf (1–2 m above ground). They fed on honeydew, preened and rested near the leaf apex. Only five females (26.3%; n = 19) took short flights to nearby leaves (8–10 cm away).

When males were then released into the cage singly, they also flew to the upper surface of a leaf, near the apex, and fed, preened and rested. When males did fly again, which they did sporadically, they flew in a zig-zag pattern at a height of 1–2 m above the ground and they flew around the tree canopy. In most matings that ensued (64%, n = 14) males thus approached females. In only four cases did females (29%, n = 14) land on a male's leaf, where mating took place. The male and female of the remaining pair landed simultaneously on a leaf before mating. In those cases in which males flew to a female, the time from release of the male to contact with a mate varied from 18 to 90 min (mean ± SE = 43.7 ± 7.77, n = 9), which was not significantly different (t = −0.051, P = 0.96) from the time between release of a male and a female approaching that male (42.8 (± 9.68, n = 4) min)). Most matings (86%, n = 14) took place on the upper leaf surface, and mating never took place below a height of 1 m.

When males were released before females they also flew to the upper surface of a leaf about 1.5–2 m above the ground and fed on honeydew before preening, resting and flying. Males flew much longer distances than females and they flew in a zig-zag pattern around the tree canopy. Two males landed on leaves where other males were resting and performed typical premating wing vibrations. They did not try to copulate and soon flew away.

On being released individually into the cage with males, females landed on the upper surface of a leaf 1–2 m above the ground, where they fed, preened and rested. Some females (35%, n = 20) flew in a zig-zag pattern around the tree canopy and landed on leaves where males were resting. The males immediately vibrated their wings and all of these pairs then copulated. The time females spent in flying before landing alongside a mate varied from 5 to 25 min (mean ± SE

Table 1. Response of *Diachasmimorpha kraussii* males to females recently killed by freezing (control) and to freeze-killed females soaked in acetone to remove cuticular lipids and with their ovipositor removed to alter their visual appearance.

	n	Wing vibration	%	Mounting attempted	%
Control	22	22	100	22	100
Acetone soak (Ac)	22	15	68	11	50
Ovipositor off (Oo)	26	24	92	15	58
Ac + Oo	26	6	23	3	12

= 12.9 ± 3.05, n = 7). Most females (65%, n = 20) did not fly again after their initial landing, and they were located by males in zig zag flight. The time between female release and a male landing alongside a female varied from 3 to 129 min (mean ± SE = 36.6 ± 9.36, n = 13), and was not significantly different (t = −1.813, P = 0.087) from the time preceding mate finding by females. Again, mating usually took place on the upper surface of a leaf (95%, n = 20), and never took place lower than 1 m from the ground.

Combining the results across experiments shows that males located females much more frequently than females located males (67% vs 33%, n = 33). The average time for males to locate a female did not differ across experiments (t = −0.54, P = 0.59). Those females that located males did so significantly faster when females were released after males (t = −3.68, P = 0.005), but sample sizes were low.

The Stimulus for Male Wing Vibration.—No males showed courtship behavior when left alone in clean mating units (n = 9) or when exposed to a container that had held 0.5 ml acetone (n = 9). Also, no males vibrated their wings in response to males recently killed by freezing (n = 10) or to males soaked in acetone after being killed by freezing (n = 10). By contrast, males presented with females recently killed by freezing, all showed the usual pattern of wing vibration (i.e., several series of wing vibrations) and each mounted the female (n = 22). Whereas males vibrated their wings in response to living females (n = 22) at a mean (± SE) distance of 10.2 (± 0.064) mm for living females, they did so at a significantly greater distance from dead females (mean ± SE = 13.2 ± 0.094, n = 20) (Wilcoxon two-sample test, t = 0.0153, P = 0.011).

When males were provided with recently frozen females that had been soaked in acetone, 68% of them vibrated their wings, but only 50% mounted the females (Table 1). Almost all males vibrated their wings in response to females recently killed by freezing and with their ovipositor removed, but almost half of them did not mount the females (Table 1). After the females without ovipositors had been soaked in acetone, the number of males that responded was reduced drastically; only a quarter of them vibrating their wings and 12% mounting (Table 1).

Twenty per cent of males vibrated their wings when placed in vials containing extracts from crushed females (n = 10), but they made only one brief burst of wing vibration. All males vibrated their wings and all mounted the female if only her head and thorax was provided (n = 10). Although all males vibrated their wings when presented with just the abdomen of the female, only two tried to mount (n = 10).

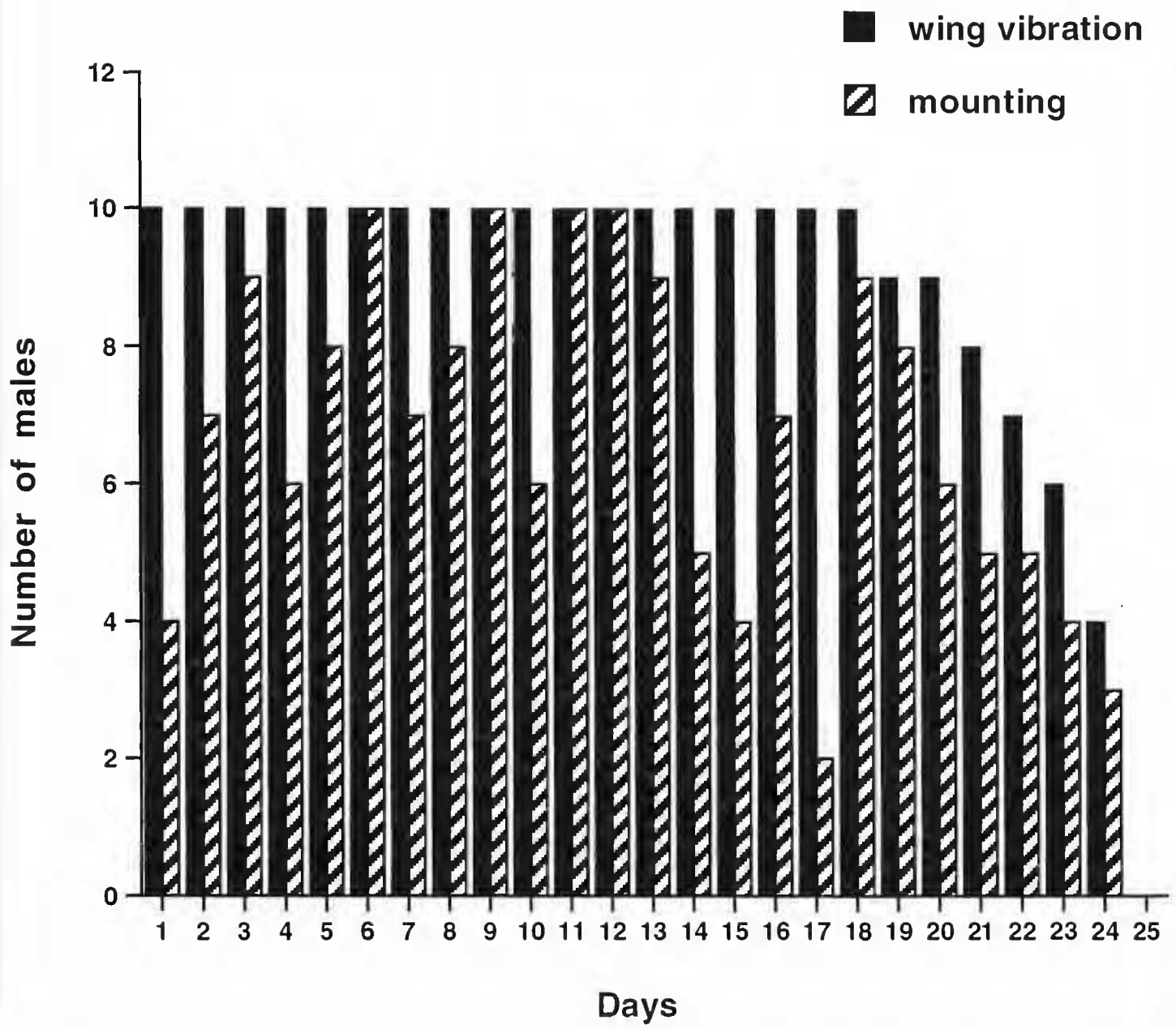

Figure 1. Positive behavioural response of *Diachasmimorpha kraussii* males to dead females. The same set of dead females was used throughout whereas a new set of males (n = 10) was exposed to the females each day. Only one pair of wasps was held in each vial.

When a set of dead females (one per vial) was exposed each day to a newly-emerged male (one per female), all males vibrated their wings each day for the first 18 days of exposure (Fig. 1), but the number responding declined from day 19, and by day 25 no males responded. The number of males attempting to mate varied considerably (Fig. 1).

Role of Male Wing Vibration.—When males' wings were removed, the percentage that achieved intromission was reduced drastically. No females showed receptive behavior in response to wingless males, but just walked and preened. Nevertheless, three of the wingless males (18.8%, n = 16) were able to mate. The other 13 walked around, but did not attempt copulation. By contrast, most control males (80%, n = 10) mated successfully, despite their prior immobilization in a freezer. The two males that did not mate successfully nevertheless displayed typical wing vibration in response to the presence of the virgin females.

Female Premating Period and Polyandry.—About a quarter of females mated as soon as six hours after eclosion, and all had mated by the time they were two days old (Fig. 2). Regardless of age, all virgin females mated when exposed to

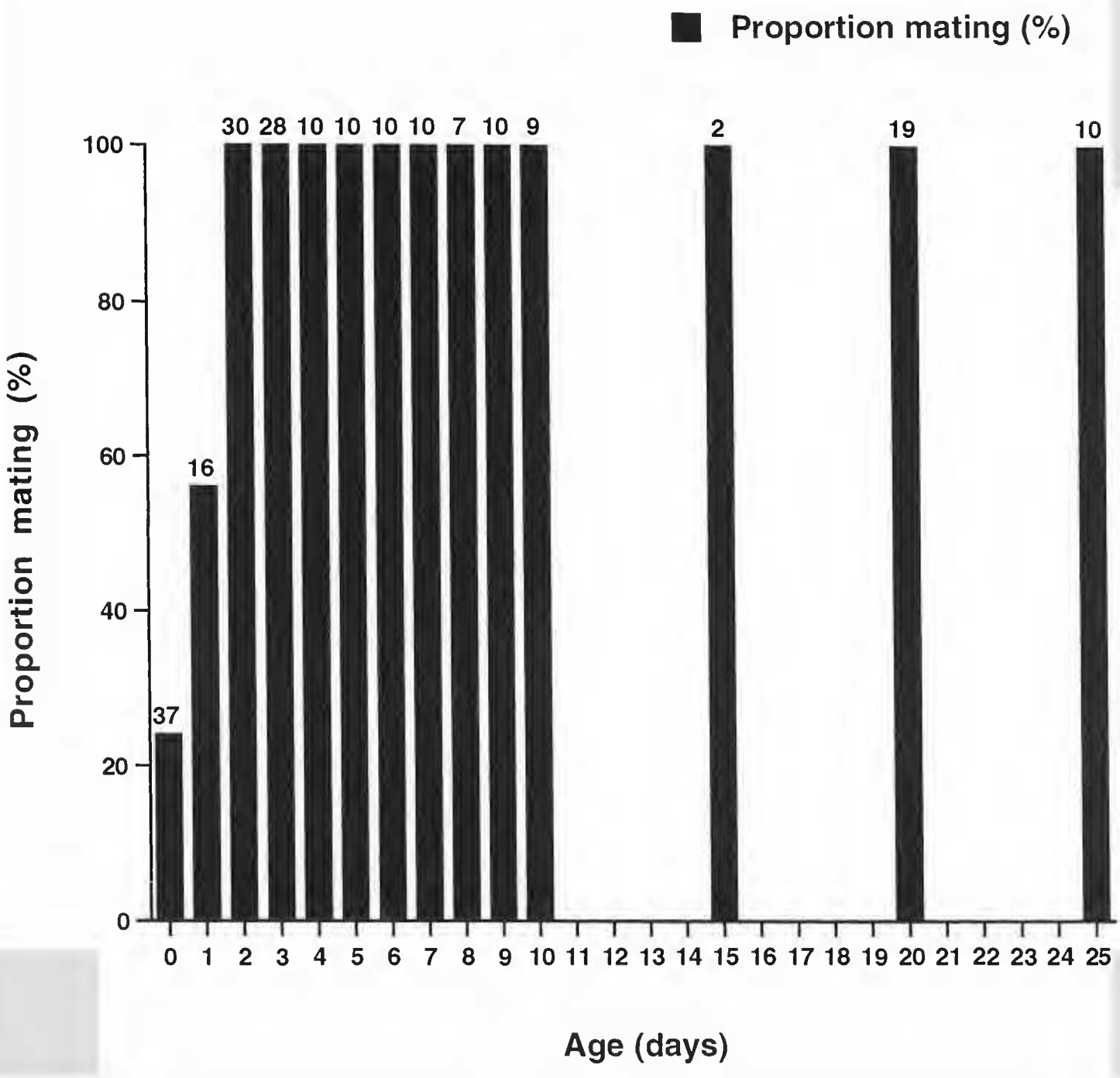

Figure 2. The percentage of virgin female *Diachasmimorpha kraussii* of different ages that mated within 10 minutes on first exposure to conspecific males. The number of wasps observed on each occasion is presented above each bar.

males (Fig. 2). None of the females that were mated one day after emergence mated again, whether at seven days (n = 17), 15 days (n = 6) or 20 days (n = 3).

Is Mating Strictly Diurnal?—Under low light intensity (0.35 lux) only four pairs (28.5%) of *D. kraussii* mated (n = 14). The behavior of these males and females was normal in all respects. The males in the ten pairs that did not mate initially in the field did not vibrate their wings in response to female presence. However, they did so in the laboratory, where light intensity was 11 lux, and all of them mated.

Cross-mating Experiment.—Superficially, the mating behavior of *D. longicaudata* resembles that of *D. kraussii*, but durations were not measured. In the cross-mating tests, when *D. kraussii* males (n = 20) were exposed to *D. longicaudata* females, they vibrated their wings in the same way as when exposed to *D. kraussii* females, but none attempted to mate (Table 2). When *D. longicaudata* males (n = 20) were in the same mating unit as *D. kraussii* females, all of the males vibrated their wings and 60% of them attempted copulation despite the females

Table 2. Results of a cross-mating test between *Diachasmimorpha kraussii* (K) and *D. longicaudata* (L). Control crosses were conducted simultaneously. All wasps were virgin, males were one day old and females two days old. $n = 20$ pairs in each test.

Test crosses	% Males involved in: Wing vibration	Mounting attempts	Intromission
♂ K × ♀ K	100	100	100
♂ L × ♀ L	100	100	100
♂ K × ♀ L	100	0	0
♂ L × ♀ K	100	60	0

not taking up the usual posture that indicates receptivity. No females allowed a non-conspecific male to copulate. When *D. longicaudata* males tried to copulate with *D. kraussii* females, the females did not stand still but walked around and sometimes vibrated their wings. Conspecific males and females in the control crosses mated normally when they were placed together in a mating unit (Table 2).

Discussion

The SMRS of *D. kraussii* is a sequence of steps involving olfactory, visual and acoustic signals, as summarized diagrammatically in Fig. 3. This synthesis is hypothetical, and is designed to help visualise the relationship among components of the overall interaction, to identify areas for further research and to aid the design of comparisons among populations.

Presumably the wasps do not mate at their emergence site because most males emerge at least one day before females (Rungrojwanich & Walter 1999). Although males could wait for female emergence, this is not usual in solitary species, or even quasi-gregarious ones (Myint & Walter 1990, Nadel & Luck 1992). Also, a considerable proportion (about 30%) of the brood emerged at irregular intervals after the main emergence (Rungrojwanich & Walter 1999) and they would be less likely to find mates at the emergence site. Possibly there is a particular part of the environment to which both sexes would be attracted and where mating would take place, as proposed for the pteromalid parasitoids *Spalangia cameroni* (Perkins) (Myint & Walter 1990) and *Pachycrepoideus vindemiae* (Rondani) (Nadel & Luck 1992). In *D. kraussii* one or more particular host plant species may attract males and females, or the environmental cue may be more general, perhaps any tree with fruit attacked by fruit fly larvae. Observations in the field have shown that males, sometimes in considerable numbers, may fly around the canopy of fruiting host trees (brazilian cherry) during the day (M. K. Ross, personal communication), presumably waiting for females to arrive.

A combination of visual and chemical signals seems to be used once the sexes are in the same general area around a host plant. This is supported by the low frequency of mating recorded at night. In the flight cage experiment, the most common means of the sexes meeting was through males flying around the tree canopy and landing on the leaf on which a female was resting, which implies that visual and chemical cues are used for mate finding. Our behavioral observations suggest the females release an attractant volatile. Because females sometimes

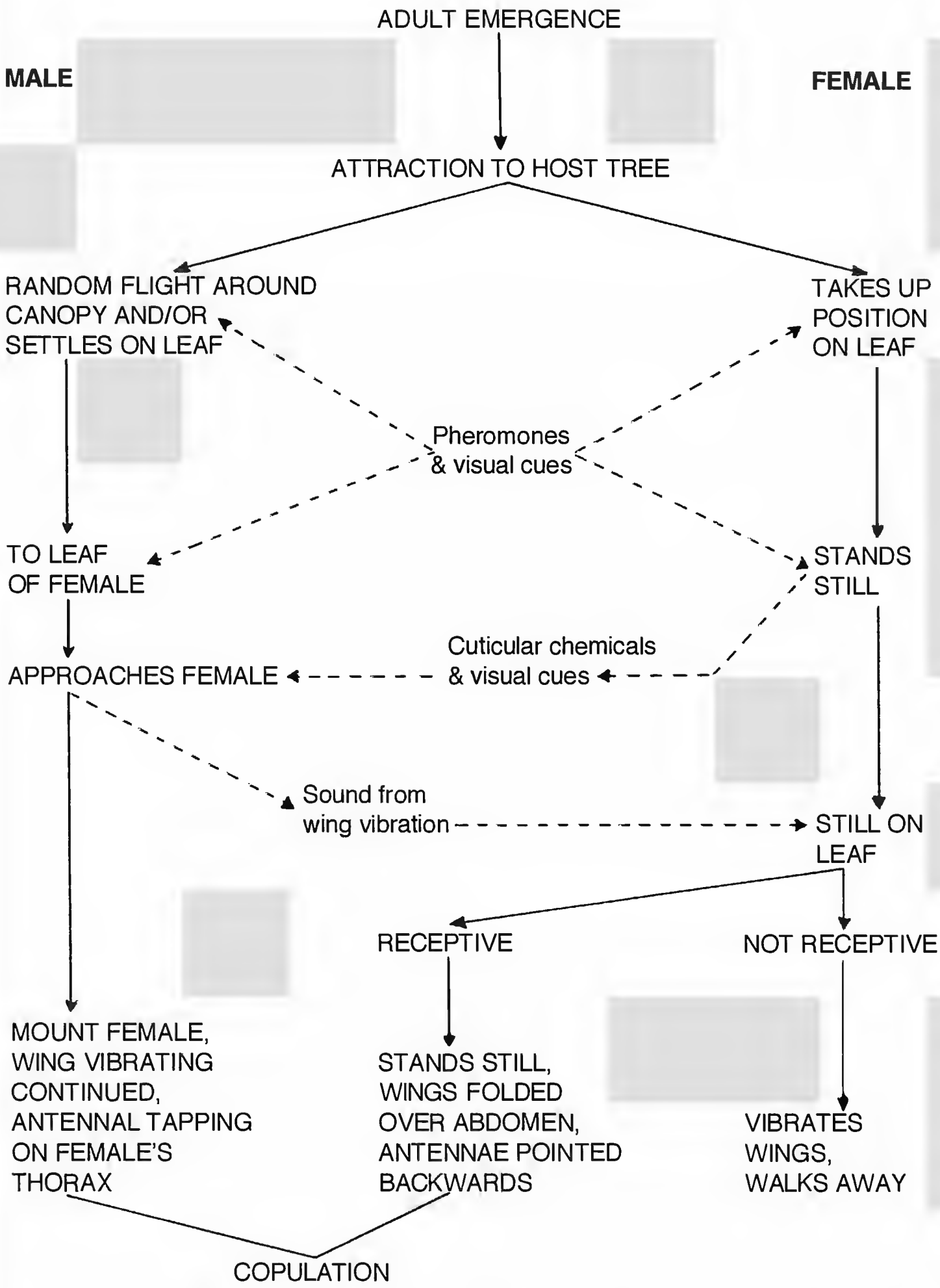

Figure 3. Postulated structure of the Specific-Mate Recognition System of *Diachasmimorpha kraussii*, an opiine parasitoid of fruit flies. See text for details of the type of evidence supporting each interpretation. Solid lines indicate transitional steps in behaviour, with arrows indicating direction. Dashed lines indicate signals between males and females. Arrows indicate the direction in which the signal acts. Bidirectional arrows imply uncertainty of signal direction.

homed in on males, both sexes may do so. Possible sex pheromones in opiines have been investigated only in males (Williams et al. 1988).

Once the sexes are in close proximity (about 1 cm) the male responds to the female with acoustic signals associated with wing vibration, as recorded for the congeneric *D. longicaudata* (Sivinski & Webb 1989). Whether the signals are airborne or vibrational (see Field & Keller 1993) has yet to be established for these opiines. The stimuli for wing vibration are relatively stable (for about 25 days: Fig. 1) chemicals associated with the female cuticle. At this stage the female, if receptive, stands still and adopts a characteristic posture while the male approaches her. Again, visual stimuli seem to be a cue for the male to locate the mating partner with whom he is interacting. The typical posture that the receptive female adopts is not critical to the recognition process itself, because the male tries to copulate even with severed parts of a female (head + thorax), and also with *D. longicaudata* females that do not adopt such a posture in the presence of *D. kraussii* males (Table 1).

No information is available on the role of tactile stimuli during courtship, mounting and copulation. Presumably tactile stimuli come into play only after males have actually mounted their mating partners. Some tactile stimuli are associated with overt behaviour. For example, the male taps his antennae on the thorax of the female during copulation. Other signals may be less obvious. For example, the position of the male's legs during intromission may be important in keeping the female passive and willing to copulate.

Finally, we confirm with behavioral evidence that the separation of *D. kraussii* from *D. longicaudata* on morphological grounds is accurate, and we predict from the behavioral observations, reported in Table 2, that the cuticular chemicals of the females of the two species will resemble one another closely, but the acoustics of the males will be different across the species.

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